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Chapter 18

The role of light in coral physiology and its implications for coral husbandry

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ABSTRACT
Light is important as a source of energy for zooxanthellate corals. A short overview is presented of the current scientific insights in the physiology of light utilisation by the coral holobiont. This information is translated into practical considerations with respect to artificial lighting in coral reef aquaria.

INTRODUCTION

Light is a key factor for the physiology of corals that contain symbiotic phototrophic micro-organisms (zooxanthellate corals). As such, appropriate lighting is crucial for growing and maintaining zooxanthellate corals in captivity. It is the aim of this paper to briefly highlight the most important theoretical aspects and practical considerations relating to light and corals. It is not our aim to present a complete literature overview on this topic, which has been intensively described elsewhere (for reviews, see Falkowski *et al*., 1990; Titlyanov and Titlyanova, 2002a; Riddle, 2007). In addition, for general information on photosynthesis in aquatic environments we recommend reading the textbook by Kirk (1983).
In the theoretical part of the paper, we describe why corals need light, how light is captured and how corals deal with changes in the light regimes that they experience. In the second part (practical considerations), we present a short overview of lighting materials for aquaria with suggestions on their utilisation.

THEORETICAL ASPECTS

Light: definitions and nomenclature

The term light usually refers to the part of the electromagnetic spectrum that is visible for the human eye (visible light). More or less the same fraction of the electromagnetic spectrum is used for photosynthesis by photosynthetic organisms and is termed Photosynthetically Active Radiation or PAR. PAR and visible light can be defined as "electromagnetic waves with a wavelength of 400 to 700 nm".
In order to quantify light, several quantities and corresponding units have been defined (see Table 1 for an overview). It is important to realize that several quantities and units commonly used in aquariology, such as luminous flux or light power (unit: lumen) and illuminance (unit: lux = lumen per m^2) have been normalized to the perception of brightness of the human eye. Since light is used in aquaria to culture corals, it is often better to quantify light from a coral point of view. As will be pointed out in subsections 2.3 and 2.4, a useful term with respect to light and corals is the photon, which is the smallest (elementary) quantity of radiation. The authors propose to use the quantity PAR intensity (also termed Photon Flux Density) and the unit µmole photons.m^{-2}.s^{-1}, also termed µE.m^{-2}.s^{-1} (one E being equal to 1 mole of photons) to quantify the light that is available for a coral on a certain spot. However, it is important to realize that this unit tells us nothing about the

Table 1: Light: terminology, quantities and units.

Term	Description	Unit
Light	Electromagnetic radiation within the visible range of 330-770 nm.	
Photon	Smallest quantity of light energy. Photons within the range of wavelengths used for photosynthesis contain just enough energy to excite one photosystem molecule.	
Luminous intensity	The power (= energy per unit of time) of light emitted by a light source into a particular direction (expressed per steradian - sr), corrected for human-eye brightness perception.	Candela (cd) = SI unit, based on a defined light source
Luminous flux	The total amount of light power emitted by a light source per unit of time, corrected for human-eye brightness perception.	Lumen (lm) = cd x sr
Luminance	The luminous intensity in a given direction.	$cd.m^{-2}$
Illuminance	The intensity of incident light per unit of surface area, corrected for human-eye brightness perception.	Lux (lx) = $lm.m^{-2}$
Luminous efficacy	Ratio between light power and total power.	$lm.W^{-1}$
Color temperature	An indicative quantity for light color.	Kelvin (K)
Irradiance*	The power of incident electromagnetic radiation per unit of surface area.	$W.m^{-2}$
PAR	Photosynthetically Active Radiation (radiation with wavelengths in the range of 400-700 nm).	
Photon flux density (PFD)**	The quantity of incident PAR per unit of surface area per unit of time.	µmol $photons.m^{-2}.s^{-1}$ or µEinstein (µE).$m^{-2}.s^{-1}$

* Also often termed “light intensity”.
** In this paper referred to as PAR intensity. We propose to use the term Photosynthetically Active Irradiance (PAI) as the quantity for measuring incident light per surface area per unit of time.

distribution of photons within the range of 400 to 700 nm (i.e. the light spectrum). There is no single conversion factor from illuminance to PAR intensity, since this is dependent on the spectrum of the light source concerned. To further complicate the issue, photons of different wavelength carry different quantities of energy: hence, conversion of PAR intensity to irradiance (in $W.m^{-2}$) is also dependent on the spectrum of the light. For more extensive definitions and conversion tables (converting photometric to radiometric units for different light sources), we refer to publications by Thimijan and Heins (1983) and Fournier (2001).

Light in aquatic systems

In nature, light is provided by the sun. Sunlight is unique in its properties; it covers a wide range of wavelengths ranging from infrared to ultraviolet. When light penetrates into (sea) water, it is attenuated. Hence, the total intensity of PAR decreases with depth. In addition, also the light spectrum changes with depth: the shorter the wavelength, the deeper the light penetrates. In clear water, blue light (400-500 nm) can still be visible at depths below 100 m, while red light (600-700 nm) almost completely disappears between 1 and 5 m. The patterning of sunlight in natural marine environments (see for example Figure 1) is nicely illustrated by Joshi (2005). Apart from the wavelength-specific attenuation of sunlight in seawater, the natural light regime also varies as a result of weather (clouds), season (day length) and the position of the sun (variation during the day).

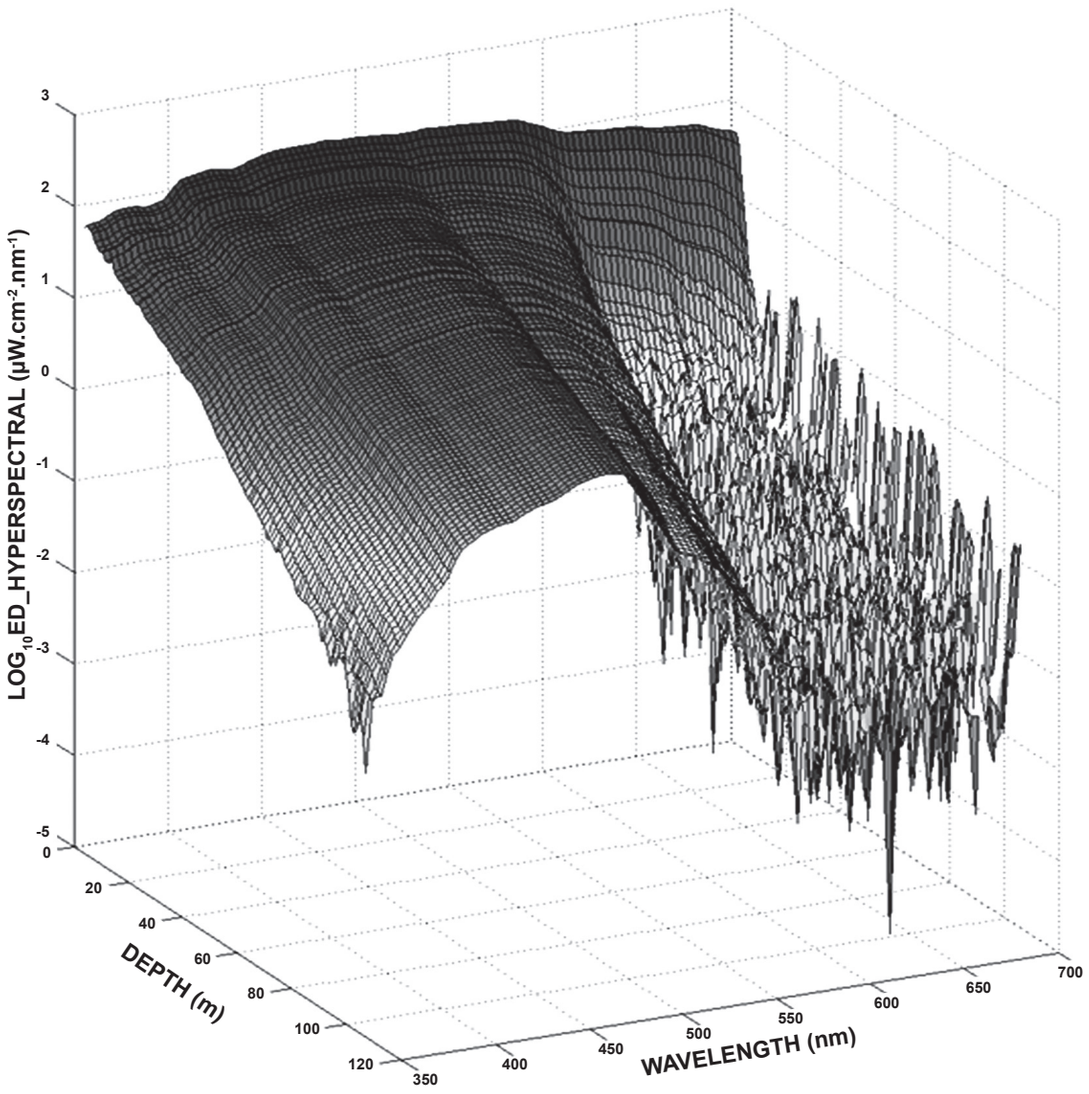

Figure 1: Example of a depth profile of PAR in the sea. Data were obtained using a Satlantic HyperOCR light profiler near Lanai Island (Hawaii Archipelago). Courtesy: Scott McLean & Robert Burns, Satlantic Inc.

A phenomenon that has recently been mentioned in relation to coral culture is the effect of rapid light fluctuations: short fluctuations in light intensity having an either stimulating or inhibiting effect on photosynthesis (Legendre *et al*., 1986). In nature, rapid fluctuations in light intensity occur in shallow waters as a result of wave motion; the irregular wave-like surface producing a focusing effect. Although we cannot exclude the possibility that these wave-induced light fluctuations have a beneficial effect on coral photosynthesis and growth, it will be very hard to prove this by sound experimental data. The frequencies of the fluctuations should specifically be above 0.1 Hz to take any effect. Moreover, the effect will not take place under diffuse light (e.g. during cloudy days or under fluorescent lighting), it will only occur under direct light (e.g. direct sunlight, direct metal halide lighting).

The variation of light in space and time has consequences for light-dependent corals. Corals have a wide range of strategies to deal with varying light regimes, as will be pointed out later in this paper.

Utilization of light: the coral – zooxanthellae symbiosis

Many scleractinian corals live in symbiosis with unicellular algae, which are termed zooxanthellae. Without exception, all coral zooxanthellae found up till now are dinoflagellate algae belonging to the genus *Symbiodinium* (Baker, 2003).

Corals containing these symbionts are termed zooxanthellate corals. They benefit from the presence of the zooxanthellae, because these symbionts transfer a significant proportion

of their photosynthetically produced organic compounds to the coral host. It has been estimated that up to 90% of the energy requirements of the coral host can be provided by their symbiotic zooxanthellae (Titlyanov and Titlyanova, 2002b).

Since light is an essential requirement for zooxanthellate corals, it is of interest to scientists and aquarists to know the relationship between PAR intensity (expressed in $\mu E.m^{-2}.s^{-1}$) and coral photosynthesis. Using Pulse Amplitude Modulated fluorimetry (PAM; see for instance Ulstrup *et al*. 2006), the rate of photosynthesis of a coral can be estimated. Riddle (2007) shows a series of PAM measurements on different coral species under increasing PAR intensity. These measurements usually give a curve as shown in Figure 2: first, there is a positive correlation between PAR intensity and photosynthesis rate: more PAR intensity results in a higher photosynthetic activity. Then, a plateau is reached (the maximal photosynthetic capacity has been reached) and at high PAR intensities, the photosynthesis rate decreases due to photo-inhibition. Riddle (2007) concluded that most coral species do not need PAR intensities higher than 300 $\mu E.m^{-2}. s^{-1}$. However, recent studies (e.g. Houlbrèque *et al*., 2004) have demonstrated that heterotrophic feeding increases the photosynthetic capacity of corals: corals obtaining additional food had higher photosynthetic rates at higher PAR intensities (starting from 300 $\mu E.m^{-2}.s^{-1}$) than starved corals. Also their maximal photosynthesis rate increased and was achieved at a higher PAR intensity (at 300 $\mu E.m^{-2}.s^{-1}$ without additional feeding and at 800 $\mu E.m^{-2}.s^{-1}$ with additional feeding). These results imply that for efficient coral growth, a combination of high PAR intensity and regular feeding is needed. Light is also known to enhance the calcification process in corals (Moya *et al*., 2006). This subject is further explained in another chapter of this book.

Absorbance of light by corals: pigments

Photosynthesis in plants takes place in specific organelles inside the plant cells termed chloroplasts. The main constituent of the chloroplasts are the thylakoid membranes, which contain pigments: molecules designed to capture light for utilisation of light energy. The mode of action of a pigment is visualized in Figure 3: when a light photon hits the pigment molecule, electrons are excited to a higher energetic state. Within the PAR range, each photon carries sufficient energy to excite one pigment molecule, which explains our preference to use the unit $\mu E.m^{-2}.s^{-1}$ to quantify the availability of light. The excited electrons go through a series of consecutive reaction steps known as the Electron Transport Chain (ETC; this is the process quantified by PAM fluorimetry). During this reaction chain, the electrons go back to their original energetic state and ATP (metabolic energy) and NADPH (reducing agent) are formed. This is the part of the photosynthetic reaction known as the light reactions: these steps only occur when light is available. The ATP and NADPH formed during the light reactions are used to convert CO_2 into organic carbon. This part of the photosynthesis process, which is light-independent, is known

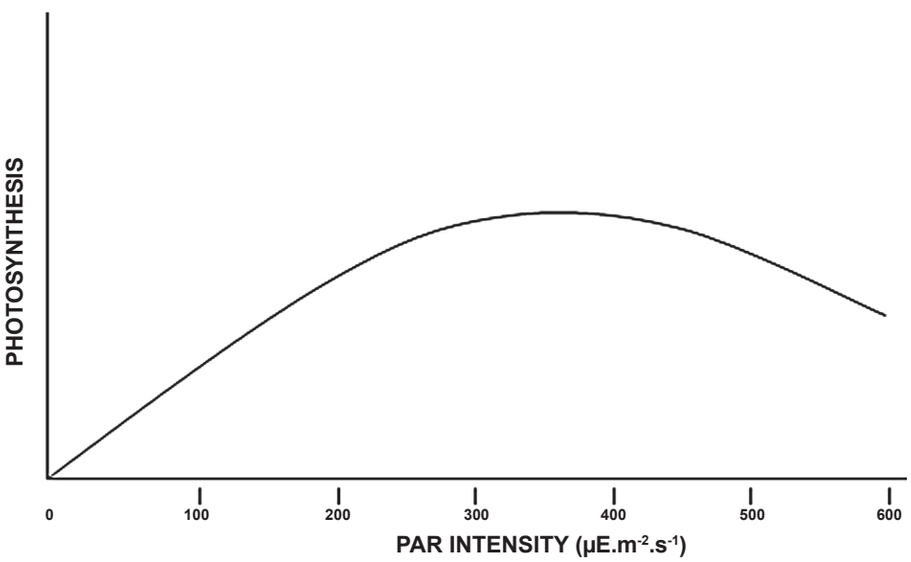

Figure 2: Theoretical relationship between photosynthesis and irradiance (PI curve). At higher irradiance, photosynthesis will be reduced due to photo-inhibition.

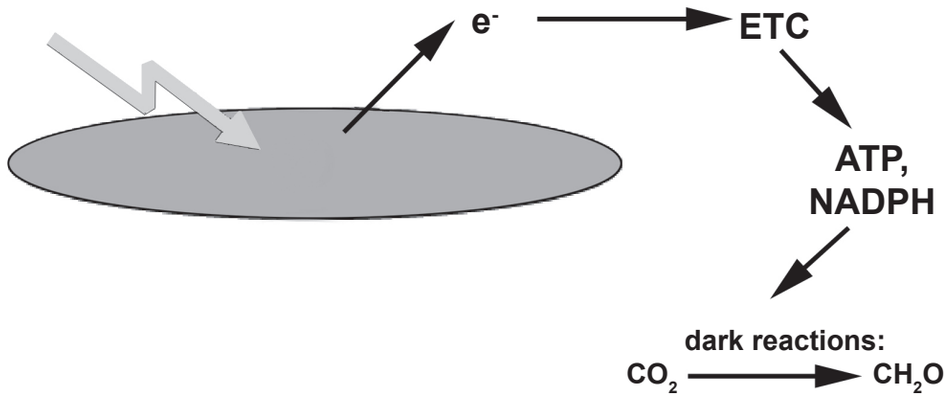

Figure 3: Simplified model of a chloroplast (grey) trapping light energy: light excites electrons (e^-) which go through several consecutive reaction steps known as the Electron Transport Chain (ETS), thus generating energy (ATP) and reductive power (NADPH) that can be used to convert Carbon dioxide into organic biomass (dark reactions).

as the dark reaction.

Many different pigments exist, which all have specific capacities with respect to light capture. These specific capacities are reflected in the absorption spectra of the respective pigments. The most well-known pigment, chlorophyll a, is most efficient with respect to energy transfer at wavelengths of 400-500 and 630-700 nm. Hence, light sources with intensity peaks in these ranges are useful to grow plants with high chlorophyll a content. Because different pigments have different absorption spectra and different organisms may contain different (combinations of) pigments, phototrophic organisms can inhabit areas with a wide range of light conditions. This also holds true for zooxanthellate corals, which occur at different depths, with light intensities ranging from 100% of the PAR intensity at the water surface (surface PAR) to less than 1 % of surface PAR (Titlyanov and Titlyanova, 2002a). Even a single species can inhabit a wide range of depths: in the Gulf of Eilat, colonies of *Stylophora pistillata* have been found at depths ranging between 1 and 66 m, with the concurrent light regime being clearly reflected in the pigmentation levels (Falkowski and Dubinsky, 1981; Dubinsky and Jokiel, 1994).

The phototrophic plasticity of corals is nicely illustrated by the work of Levy *et al*. (2003), who studied the photo-behaviour of five species of corals. In *Favia favus*, they found 5 different pigments, of which the combined absorption spectra covered nearly the entire range of PAR. A further example is presented by Myers *et al*. (1999), who compared the levels of chlorophyll and peridinin in seven species of stony corals inhabiting different depths. Differences up to one order of magnitude were found among the species studied.

Dealing with changes in light regime: photo-acclimation

As pointed out in the previous subsections, corals in the wild grow under different light regimes and experience fluctuations (clouds – clear sky; day-night cycle, season) in light intensity. In order to cope with these fluctuations, corals have developed a range of physiological mechanisms, which are collectively referred to as photo-acclimation.

We can categorise these mechanisms as follows:

- Immediate responses. Corals can rapidly contract or expand their tentacles and other tissues, thus increasing or decreasing the light-capturing surface area (Levy *et al*., 2003; 2006).
- Short term responses (days to weeks). Zooxanthellae can change their pigmentation, both the concentration and the composition. In this way, the coral can adapt within a few days to higher and lower light intensities and to changes in light composition (blue versus red light). This was shown for instance by Dustan (1982), who measured the PAR absorption capacity of isolated zooxanthellae of *Montastrea annularis*, obtained from five different depths ranging from 2.5 to 37.5 m. With increasing depth, the zooxanthellae increased their absorption capacity, in particular for blue light, but also for red light, even though red light does not penetrate to greater depths. The latter may be the result of higher levels of chlorophyll a, which absorbs both blue and red light.
- Long term responses (months to years).

- While growing, corals will adapt their growth form to the ambient conditions (Tilyanov and Titlyanova, 2002a). A specimen growing under low light will try to expose more horizontal surface to the incoming light than a specimen of the same species growing under high light, and will thus develop a more flattened shape.

The process of short-term photo-acclimation in stony corals was nicely demonstrated by Titlyanov *et al*. (2001a), who transplanted colonies of *Stylophora pistillata* growing under high light intensities (95 % of the PAR intensity at the sea surface) to lower light (30 % of surface PAR) and from 30 % of surface PAR to low (8 % of surface PAR) and extremely low light (0.8 % of surface PAR). Within 40 days after transplantation, the corals had nearly doubled their zooxanthellae density, and the concentration of chlorophyll per zooxanthellate cell volume increased with 50 %. The average volume of the zooxanthellae decreased slightly in this period. As an overall results, the corals had more than doubled the total amount of chlorophyll their polyps within 40 days. When corals were transplanted from 30 % to 8 % surface PAR, a similar response was observed. However, transplanting from 30% to 0.8% surface PAR considerably reduced the amount of chlorophyll per polyp: despite higher chlorophyll content per zooxanthellate cell and an initial increase in zooxanthellae numbers, zooxanthellae numbers dropped dramatically after ten days, indicating that this light intensity was too low for the zooxanthellae to grow.

In a consecutive study in experimental systems, Titlyanov *et al*. (2001b) demonstrated that heterotrophic feeding mediated the photo-acclimation process. Only fed corals showed complete acclimation from surface PAR to dim (20% of surface PAR) and low light (3% of surface PAR). An excellent review of these and other photo-acclimation studies is provided by Titlyanov and Titlyanova (2002a).

Interesting with respect to short-term changes in zooxanthellae is the Adaptive Bleaching Hypothesis (ABH, Kinzie III *et al*., 2001; Fautin and Buddemeier, 2004): corals may expel their entire zooxanthellae population (bleaching) as an adaptation to changes in the environment. Subsequently, the coral host will take up other strains of zooxanthellae (that are better adapted to the new circumstances) from the environment. Although adaptive bleaching is mainly described in association to changes in temperature, it may also occur as a result of changes in light regime.

The process of photo-acclimation is very relevant with respect to maintaining corals in captivity. It means that corals can cope well with changing lighting conditions (new light bulbs, movement to a new position in a tank, transfer from a high light intensity cultivation system to a lower light intensity display aquarium etc.). However, care should be taken not to impede too much light stress onto corals in captivity. This subject will be dealt with in the next section.

PRACTICAL CONSIDERATIONS

The information in the above section about photo-acclimation might suggest that corals are sufficiently flexible to withstand strong fluctuations in light regime, thus implying that lighting in coral aquaria is easy to manage. Although many corals may indeed be relatively resistant to shifts in light patterns, there are some issues to be aware of:

- Changes in environmental circumstances imposed on organisms require physiological responses, which imposes stress on the organism. Corals in aquaria may be subject to multiple stressors (e.g. insufficient food, suboptimal water movement, imbalances in water quality parameters) and may as such be more vulnerable to rapid shifts in light patterns than corals in nature.
- Up-shocks in light intensity may be more harmful than down-shocks. A shade-adapted coral that is positioned in a high-light environment without proper acclimation has a large risk of bleaching. Shade-adapted corals have a higher zooxanthellae density in their tissue and have higher pigment content per zooxanthellate cell when compared to light-adapted corals. Hence, shade adapted corals have a high photosynthethic capacity. When exposed to high light, the sudden increase in photosynthesis will cause an accumulation of reactive oxygen species, which has been reported to cause bleaching (Lesser and Farell, 2004).
- Blue light (400-500 nm) can be utilized

by almost all zooxanthellate corals. Not all corals are suited to efficiently use red light (600-700 nm), which yields less energy per photon. The use of blue light may also reduce the growth rate of fouling phototrophs such as several species of green algae and cyanobacteria, which (according to non-refereed internet sources) prefer light in the 500-700 nm range.

Artificial lighting

Several artificial light types have been developed to mimic natural sunlight in aquaria and to provide PAR to zooxanthellate corals. The internet is a plentiful source of information on light types and their respective irradiance spectra (e.g. www1; Joshi and Marks, 2004). It is not the aim of this paper to review these data. We have attempted to summarize the most relevant considerations with respect to designing and maintaining an appropriate lighting system.

Metal halide lamps and fluorescent lighting are the two most commonly used types of aquarium lighting. Metal halide lamps are point sources of light, which provide a scattering that resembles sunlight. Fluorescent lighting provides a more diffuse, uniform light pattern. For efficient fluorescent lighting, the slim-profiled T5 light bulbs (5/8 inch diameter) have been developed: they produce more photons (or lumens) per Watt than standard fluorescent bulb types (T8, T12) and have become popular among aquarists. Relatively new in aquarium technology is the use of LED lighting, which provides a uniform light pattern and an unlimited range of colour spectra.

A point of consideration with respect to the use of metal halide lamps is that they do not provide a uniform distribution of light, in particular in shallow systems. This is demonstrated in Figure 4, where the spatial light intensity distribution under an metal halide lamp (Aquamedic Aqualine 400 W, 13,000 K) is shown. Light intensity was measured 50 cm under the lamp in a shallow backstage coral cultivation tank in Burgers' Zoo (water depth of 20 cm) using a Licor LI-192 underwater cosine-corrected light sensor. The pattern in Figure 4 clearly shows

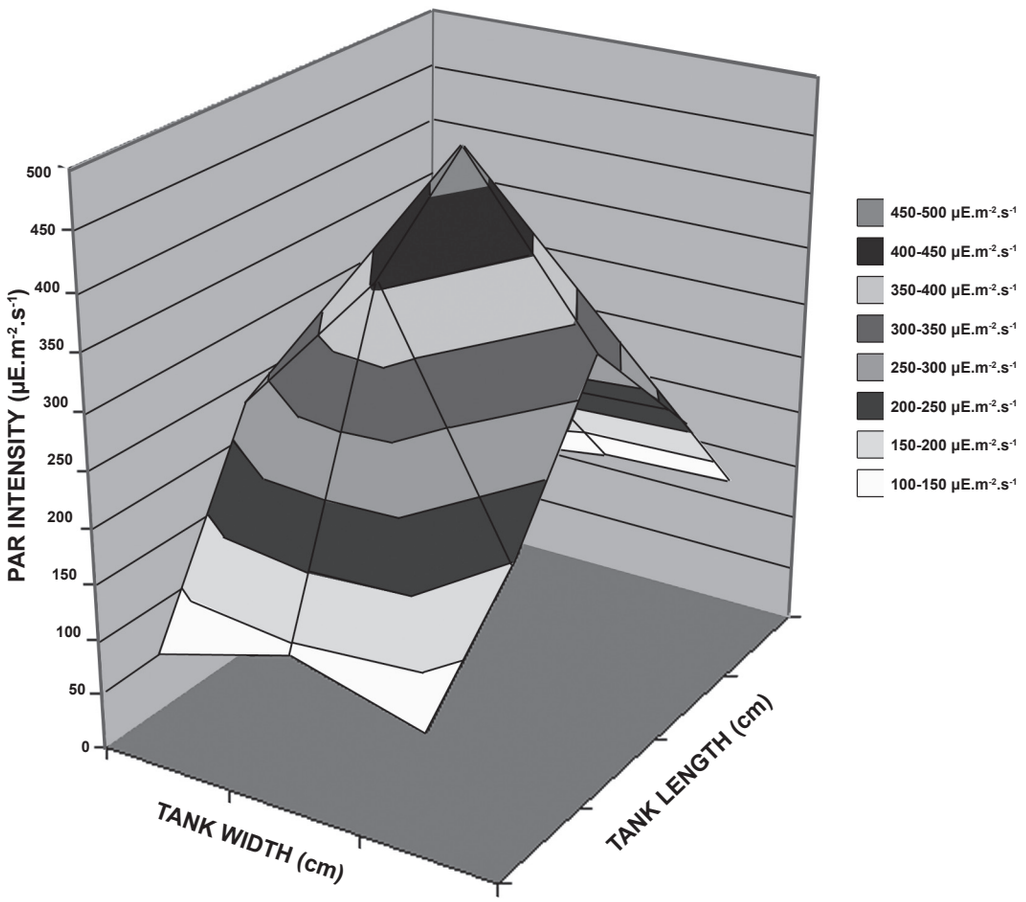

Figure 4: Spatial distribution of light intensity produced by a Metal Halide bulb, measured in a shallow tank system 50 cm underneath the light source. The lamp was positioned above the middle of the tank.

that the light intensity directly underneath the lamp is more than 100% higher when compared to the peripheral parts of the tank. This will create large differences between replicate coral colonies growing in this system.

It is well known that the quantity of light produced by light bulbs decreases in time. As an example, we measured the amount of light produced by a very popular aquarium lamp, the ATI aquablue T5 bulb during a six month period, in which the lights were switched on for 12 hours per day. Light intensity was measured with an IRRAD 2000 spectrometer (Aventes, The Netherlands). Although this method is not very accurate for quantitative irradiance determination, we found that the light intensity had substantially decreased (approximately 60%) within a six month period (i.e. after a total of approximately 2200 burning hours). We were also interested to test whether the light spectrum produced by this lamp would change over time. Hence, in addition to light intensity, also the spectrum of the T5 bulbs was measured two times (again using the IRRAD 2000 spectrometer) during the six-month experimental period. No differences of importance could be detected after a ten week period (Figure 5).

Based on the considerations above, we recommend a careful evaluation of the following points of concern when designing an appropriate lighting system for an aquarium system:

- The depth of the tank. This will determine the power needed to supply sufficient light to all parts of the tank and may also determine the light type needed: light generated by point sources such as metal halide and LED tends to penetrate deeper into the water than the more diffuse light produced by fluorescent lights such as T5. Also the spectrum is important here: for deep tanks, lights with high peaks in the blue range (400-500 nm) should be used.
- The coral species to be cultured. Each species has an optimum with respect to light intensity and the colour spectrum to be applied. If deep water species are to be cultured in a shallow tank, the light spectrum applied should resemble the deep-water spectrum.
- The purpose of the tank (display, mass cultivation, research). For displays, metal halide provides a light effect that is considered as very attractive by most spectators. In shallow system for mass cultivation or research, fluorescent light provides a uniform lighting pattern.
- The lifetime of the light bulbs, which is relevant with respect to maintenance procedures (a short bulb lifetime requires an easy replacement procedure) and costs (see below).
- The costs of the lighting system, which is

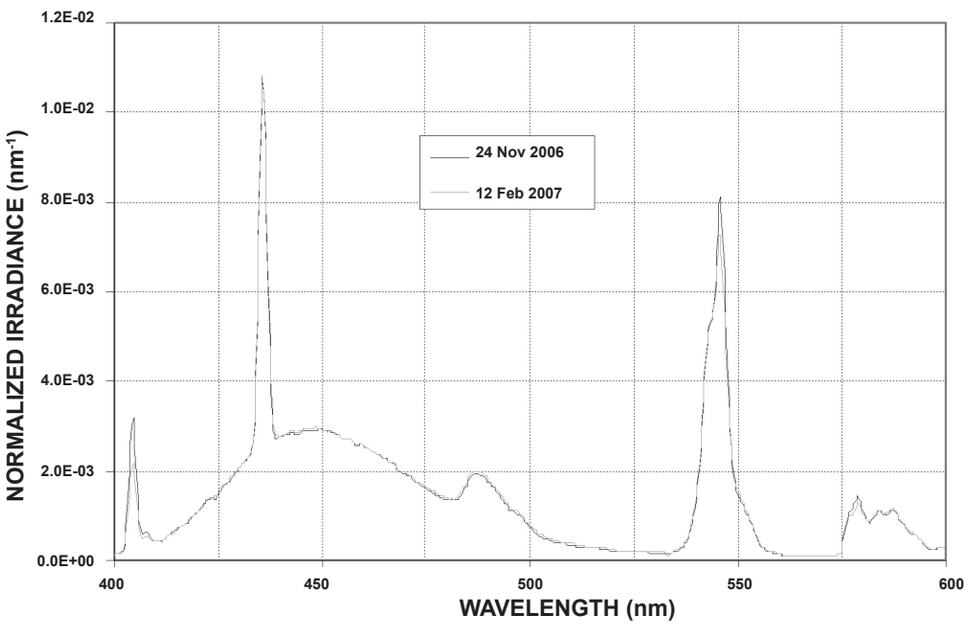

Figure 5: Spectrum of PAR produced by 4 ATI Aquablue 24 W lamps measured at the beginning and the end of a 10 weeks time interval. In order to compare the two spectra, the data have been normalized by dividing the measured irradiance per nm (in $\mu W.cm^{-2}.nm^{-1}$) by the total irradiance of the entire range of wavelengths measured by the detector (in $\mu W.cm^{-2}$).

a combination of the costs for hardware and installation, the power input needed and the lifetime of the bulbs. For instance, the use of LED lighting requires a high initial investment, but the lifetime of the LEDs is much longer than that of conventional light types and it is expected that in the near future, LED technology will become much more efficient with respect to energy consumption than fluorescent light.

Influence of cover materials

Safety first! Since seawater and electrical current are a risky combination, it is essential to safely mount the lamps, preventing any contact with seawater. For this reason, lights are usually protected with glass or Perspex (plexiglass) covers. However, these covers may reduce the penetration of light into the tank, both quantitatively (lower intensity) and qualitatively (high absorption of specific parts of the light spectrum by the cover material). We studied this potential loss of light by measuring the intensity and the spectrum of two commonly used fluorescent light tubes (ATI Aquablue 24 Watt, a T5 aquarium light and Sylvania CF-LE 55 Watt, a lamp for cultivation of algae and other plants) with and without covers. As cover materials, 6 mm thick glass and Perspex plates were used. Light spectra were measured using an IRRAD 2000 Spectrometer (Avensis, The Netherlands). For both lamps, only a minor fraction of the irradiance is lost when the cover materials are applied (Figure 6). Glass has a slightly higher quenching (10% in the 430-480

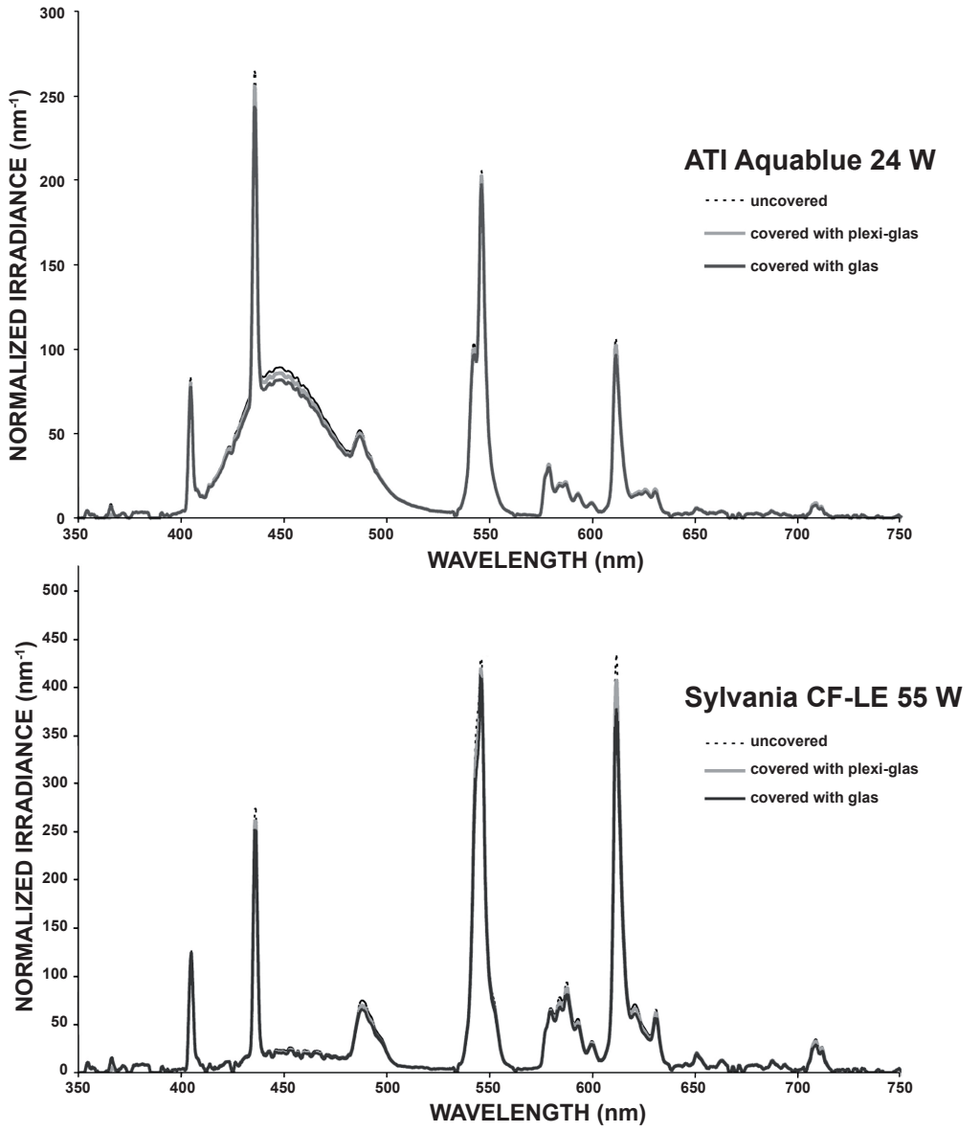

Figure 6: Spectrum of PAR produced by 2 lamp types: ATI Aquablue 24 W (upper graph) and Sylvania CF-LE 55 W (lower graph). Both lamps were measured uncovered and covered with either glass or plexi-glass (perspex) cover materials. Data have been normalized as described at Figure 5.

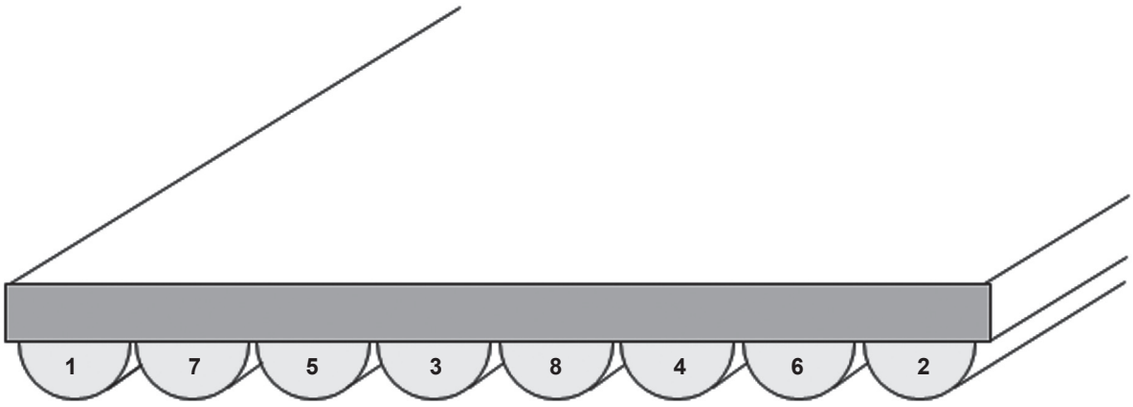

Figure 7: Example of a lighting strategy: in a lighting system consisting of eight separate TL light bulbs, one of the bulbs is replaced every two weeks. The bulb numbers indicate the order in which the bulbs are replaced. In this way, a constant, uniform light pattern is created.

nm range) than Perspex (4% in the 430-480 nm range). The observed losses do not show large differences within the range of PAR. We conclude that the cover materials applied have a negligible effect on the quality and the quantity of the light provided.

Lighting strategies

Because the quantity of light produced by light bulbs decreases in time (Section 3.1), they need to be replaced with regular time intervals. Changing all light bulbs at the same time can cause a significant light up-shock that may be detrimental to the corals. It is therefore better to replace the light bulbs in a semi-continuous way. In our research facility, where we have a system consisting of eight fluorescent T5 bulbs, we replace one bulb every two weeks (i.e. each bulb is used for 16 weeks) according to the schedule presented in Figure 7. In this way, the average light intensity in the system is kept at a very constant level both in time and space, which is desirable for research purposes and to prevent light up-shocks after bulb-replacement.

In system with a high load of phototrophic organisms (such as shallow mass cultivation systems with a high biomass to water ratio), strong fluctuations in dissolved oxygen concentrations and alkalinity may occur as a result of high photosynthesis during the day and high respiration activity during night time. An effective strategy to mediate this process is to create opposite day-night cycles in different parts of these systems. In this way, high production of oxygen and high consumption of carbon dioxide in one part of the system is compensated by high oxygen consumption and CO_2 production in the other part.

CONCLUSIONS

Zooxanthellate corals show a remarkably high plasticity with respect to utilisation of light. Despite that plasticity, care should be taken to provide appropriate lighting to corals in captivity in order to sustain growth and minimise stress. There are many good products on the market with respect to aquarium lighting. When properly designed, an aquarium system can sustain cultivation of zooxanthellate corals very well ("We are very good in growing zooxanthellae"- Bruce Carlson), although the role of appropriate feeding in stimulating phototrophic growth of corals has been somewhat neglected in aquariology.

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